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Statistical complexity of neural spike trains

Sarah Marzen, Michael R. DeWeese and Jim Crutchfield

Summary. We present closed-form expressions for the entropy rate, statistical complexity, and predictive information for the spike train of a single neuron in terms of the first passage time probability distribution. Our analysis applies to any one-dimensional neural model where observation of a spike causes the neuron to “reset” to some membrane voltage and in which any noise term is uncorrelated in time. We then use these formulae to study the linear leaky integrate-and-fire and quadratic integrate-and-fire neurons driven by white noise in the natural spiking regime. The statistical complexity [2, 1] is simply related to the interspike interval’s mean and coefficient of variation. The excess entropy, or the total predictive information, is highest for neural spike trains with low interspike interval coefficients of variation. Both the statistical complexity and the excess entropy arise naturally in the context of predictive rate-distortion and could be useful for characterizing “predictor” neurons [3] that learn to predict other neurons.

Additional Detail. The statistical complexity C_μ , predictive information $I_{pred}(T)$, and entropy rate h_μ are basic metrics that can be used to characterize a neural spike train: h_μ and $I_{pred}(T)$ are useful for characterizing the entropy of a neural spike train and, thus, useful for calculating the mutual information between the stimulus and a neural spike train; C_μ reveal underlying dynamical phase transitions and so qualitative changes in memory architecture. These quantities also offer fundamental structural interpretations: the statistical complexity is the amount of memory required to optimally predict the future; the excess entropy $\mathbf{E} = \lim_{T \rightarrow \infty} I_{pred}(T)$ is the amount of future information that is predictable. Hence, C_μ , $I_{pred}(T)$, and h_μ can characterize the performance of predictor neurons, for example [3].

However, calculating these quantities can be challenging, except in the structureless case of the Poisson neuron. Then, C_μ and $I_{pred}(T)$ vanish, and

the differential entropy rate in bits per second is $h_\mu = -\lambda \log_2 \lambda$, where λ is the Poisson process rate. We present new formulae for C_μ , $I_{pred}(T)$, and h_μ of a neural spike train whose interspike intervals are drawn independently from some distribution $F(t)$. This includes neural spike trains of both integrate-and-fire neurons and spike-response time neurons driven by white noise. Denote the mean interspike interval as $\langle T \rangle$ and define $w(t) = \int_t^\infty F(t')dt'$, $Z = \int_0^\infty w(t')dt'$. When the time resolution Δt of the observer is very small,

$$C_\mu = - \int_0^\infty \frac{w(t)}{\langle T \rangle} \log_2 \frac{w(t)\Delta t}{\langle T \rangle} dt \quad (1)$$

$$h_\mu(t) = \frac{w(t)}{\langle T \rangle} \log_2 \frac{e^2 \langle T \rangle \int_t^\infty w(t')dt'}{w(t)^2 \Delta t} - \frac{1}{\langle T \rangle} \int_0^t F(t') \log_2 \left(\frac{F(t')\Delta t}{e} \right) dt'. \quad (2)$$

The entropy rate is $h_\mu = \lim_{t \rightarrow \infty} h_\mu(t)$ and the predictive information/finite-time excess entropy can be calculated from $I_{pred}(T) = \int_0^T (h_\mu(t) - h_\mu)dt$. The key to deriving these expressions was proving that the causal states [2, 1] of such a neural spike train were counts of the time since the last spike.

We present preliminary results for the linear leaky-integrate and fire model and the quadratic integrate-and-fire model with $\eta(t)$ as white noise, so that the membrane voltage follows the equation $\frac{dV}{dt} = f(V) + g(V)\eta(t)$. When V reaches V_{peak} , then a spike is emitted and V is reset to V_{reset} . First passage time probability distributions and their cumulative distribution functions were calculated empirically by generating 10^5 trajectories for each set of parameters using an Euler integration scheme. The linear leaky integrate-and-fire model can be described by $V_{peak} = 1$, $V_{reset} = 0$, $g(V) = a$, $f(V) = b - V$ with $a \geq 0$ and $b \in (-\infty, \infty)$; we studied $a \leq 5$ and $1 < b \leq 5$. The quadratic integrate-and-fire can be described by $g(V) = a$, and $f(V) = b + V^2$ for a range of $a \geq 0$ and $b \in (-\infty, \infty)$; we set $V_{peak} = 100$,

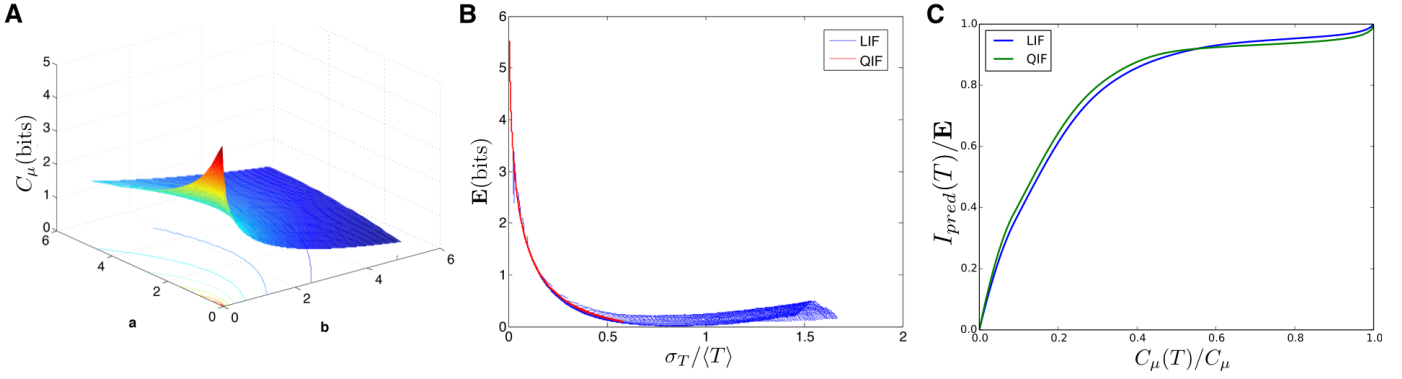


Fig. 1: **A: Differential statistical complexity of a quadratic integrate-and-fire neuron.** C_μ peaks near the dynamical phase transition at $b = 0$. **B: Excess entropy of integrate-and-fire neurons.** At low interspike interval coefficient of variation ($\frac{\sigma_T}{\langle T \rangle}$), the excess entropy appears to be a function only of the coefficient of variation. Data from linear leaky integrate-and-fire neurons are blue and data from quadratic integrate-and-fire neurons are red. **C: Predictive rate-distortion curve using finite-time causal states as predictive features.** For linear and quadratic integrate-and-fire neurons with $E \sim 0.3$ bits and $C_\mu \sim 12$ bits, assuming a time step of $\Delta t = 10^{-4}$, most of the excess entropy can be captured using only 50% of its statistical complexity. Linear leaky integrate-and-fire data is blue; quadratic integrate-and-fire data is green.

$V_{reset} = -100$ and studied $a \leq 5$ and $0 < b \leq 5$. Time is in units of the membrane time constant.

The differential statistical complexity C_μ (ignoring the Δt component of C_μ in Eq. 1) was well-approximated by

$$C_\mu \approx \log_2 \langle T \rangle + 1.4 \frac{\sigma_T}{\langle T \rangle}, \quad (3)$$

where $\langle T \rangle$ is the mean interspike interval and $\frac{\sigma_T}{\langle T \rangle}$ is the interspike interval coefficient of variation for both the leaky linear integrate-and-fire neuron and the quadratic integrate-and-fire neuron across the entire simulated parameter space. The $\log_2 \langle T \rangle$ term is the statistical complexity of a periodic signal with period $\langle T \rangle$, and the additional term $1.4 \frac{\sigma_T}{\langle T \rangle}$ accounts for the fact that the signal is *almost* periodic. For both types of neurons, C_μ is maximized at the dynamical phase transition boundary; this is shown for the quadratic integrate-and-fire in Figure 1A. Figure 1B shows that the excess entropy E increases as the interspike interval coefficient of variation decreases, which is what one would expect for an almost periodic signal. The differential entropy rates h_μ of the integrate-and-fire neurons decreased as the intrinsic noise parameter a approached 0 and the spike train became a noiseless periodic signal.

One does not need to capture all of the statistical complexity in order to capture most of the predictive information; the tradeoff between pre-

dictive ability and memory storage can be quantified by the predictive information bottleneck framework, for instance. Finite-time T causal states are (suboptimal) lossy predictive features with which we can capture $I_{pred}(T)$ of the full excess entropy E using only $C_\mu(T) = -\int_0^T \frac{w(t)}{\langle T \rangle} \log \frac{w(t)\Delta t}{\langle T \rangle} dt - \frac{\int_T^\infty w(t)dt}{\langle T \rangle} \log \frac{\int_T^\infty w(t)dt}{\langle T \rangle} + \frac{\int_0^T w(t)dt}{\langle T \rangle} \log \frac{1}{\Delta t}$ of the full statistical complexity C_μ . The quadratic integrate-and-fire neuron has a similar predictive rate-distortion curve to the leaky linear integrate-and-fire neuron at low (~ 0.1) interspike interval coefficients of variation. Figure 1C shows that, for these neurons, at least 90% of the total predictability can be captured with a memory of only $\sim 50\%$ of the total statistical complexity.

References

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